

Fauna of the grassland-forest landscape mosaics of the Bunya Mountains, eastern Australia

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ABSTRACT

Fauna assemblages were assessed within four primary vegetation types and three edge types between grassland and wooded habitats within the Bunya Mountains of eastern Australia. Wet rainforests differed in their species assemblages to dry rainforest, savanna woodland and grassy bald. Dry rainforests and savanna woodlands had similar species composition despite their dissimilar floristic and structural attributes. The small grassy balds supported lower vertebrate species richness and abundance and were significantly different in species composition to all other vegetation types. The small and structurally simple grassy balds contained a subset of species also found in surrounding forest and woodland vegetation, with only a few grassland specific species. Fauna assemblages in grassy bald-rainforest edges were significantly different to grassy balds and rainforest interiors, while grassy bald-savanna woodland edges were similar to savanna woodland interiors. The reptile *Lampropholis colossus*, the only endemic on the Bunya Mountains, was not a grassland specialist but was found in dry rainforest edge adjacent to balds, dry rainforest and savanna woodland containing rainforest elements at high altitude. A paucity of grassland specialists and endemics associated with balds concurs with evidence that grassy balds are of a relatively recent origin. Management intervention to preserve grassy balds will sustain small biodiversity gains.

Key words: Fauna, species richness, species abundance, grassland, mosaic, rainforest, savanna, woodland, montane, habitat structure.

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Introduction

Spatial mosaics of vegetation communities have a crucial effect on species diversity in the landscape (Wiens 1989; Rosenzweig 1995). This is because patches of different vegetation types can be variable in their vertical layering (MacArthur *et al.* 1966), distribution and size of trees (MacNally 1990), presence and abundance of vines (Kikkawa 1982) and the nature and extent of ground cover and litter (Martin and Green 2002). These factors can have some important influences on fauna composition and an increase in species richness with increasing structural complexity seems to be a general rule (MacArthur *et al.* 1966; Karr 1971; Holmes *et al.* 1979; Kikkawa 1982; Wiens 1989). In addition to spatial heterogeneity of structure, edges or ecotones contribute their own species assemblages that can be different to those present either side of the divide (Murcia 1995; Luck *et al.* 1999; Harper *et al.* 2005). This may increase diversity by attracting suites of edge specialising species or decrease diversity through dominance by an edge specialist that excludes other species, such as the Noisy Miner *Manorina melanocephala* of sub-tropical and temperate Australian environments (Piper and Catterall 2003).

In montane landscapes, different forest types and treeless grassland can occur in fine-scaled mosaics and are ideal for investigating fauna responses to habitats, their spatial

extent and the boundaries between habitats. Occurrences of complex vegetation types at high elevation are of international interest because they can contain relict ecosystems and endemic species that have resisted the effects of past climate change (Rowe *et al.* 2010). Specialist endemic species that are restricted in their distribution are important indicators of ancient origins. Some natural grassland possesses distinct assemblages of flora and fauna that indicate that they have evolved over long time frames, dating from the Pleistocene (Bond and Parr 2010). Montane grasslands embedded in a matrix of forest, known as grassy balds occur on a number of continents and islands worldwide (Fensham and Fairfax 1996a; Overbeck *et al.* 2007; Bond *et al.* 2008; Bond and Parr 2010). These grasslands exist in environments that could support forest yet are maintained in a grassland state. Climate, soil, topography, fire, clearing and grazing have variously been considered to explain the origins and maintenance of montane grassy balds and while the causal factors are not always clear there is increasing evidence that fire plays a role in maintaining grassy balds and the distribution of rainforest in some landscapes (Fensham and Fairfax 1996a; Moravek *et al.* 2013).

The Bunya Mountains of central eastern Australia contain grassy balds embedded in wet and dry rainforests, and

savanna woodland. These grassy balds are exceptional in that they occur within a narrow climatic band wet enough for forest but also dry enough for grassland (Butler *et al.* 2014). The Bunya Mountains landscape has had a long history of anthropogenic use because of their iconic Bunya Pines *Araucaria bidwillii* (Figure 1) which have been a focus of Aboriginal people who assembled periodically in significant gatherings to collect their nuts for food (Humphries 1992). There is increasing evidence that fire used by these Aboriginal people has helped to sustain the grassy balds of the Bunya Mountains (Fensham and Fairfax 1996a and b, 2006; Butler *et al.* 2006; Fairfax *et al.* 2009; Moravek *et al.* 2013; Butler *et al.* 2014). There is also evidence that a decrease in indigenous burning practices since the late 19th century is implicated in a substantial decrease in the area occupied by grasslands because it has led to resumption of the grassy balds by rainforest vegetation and eucalypts (Fensham and Fairfax 1996a, 2006; Fairfax *et al.* 2009). The loss of grassy balds in this landscape has important cultural significance and has the potential to reduce landscape diversity.

There is furthermore a concern that changes to landscape composition (i.e. reduction in area and number of grassy balds) will reduce biodiversity of flora and fauna on the Bunya Mountains. Without a clear picture of how fauna associates with vegetation communities it is difficult to predict the biodiversity outcomes under various vegetation loss scenarios. Few studies have provided systematic assessment



Figure 1. Iconic Bunya Pines *Araucaria bidwillii* emerge from wet rainforest adjacent to a grassy bald in the Bunya Mountains, Queensland. Photo by Michael Mathieson

of the composition and habitat use of fauna across fine-scaled mosaics of natural grasslands and forests, particularly within sub-tropical montane environments (Hagger *et al.* 2012). The Bunya Mountains is no exception. Although the fauna of the Bunya Mountains is reasonably well known due to the interests of naturalists for over a century (WildNet database, Queensland Government) there have been no previous surveys of terrestrial vertebrates conducted using a stratified systematic approach across vegetation and habitat types to assess vegetation associations. Furthermore records of fauna on the small grassy balds are scant, possibly because they have been poorly surveyed. The potential impact of grassy bald loss on fauna has therefore not been adequately assessed.

We studied the role that major vegetation types play in contributing to biodiversity in the Bunya Mountains, particularly focusing on grassy balds and abutting forest edges, to ascertain whether: 1. they act as a refuge for specialist grassland fauna; 2. they feature as subsidiary habitat for otherwise rainforest or woodland occurring species; and 3. fauna species may be lost if grassy balds were to disappear from this landscape.

Methods

The Bunya Mountains are an isolated basaltic massif where the headwaters of Murray-Darling, Brisbane and Burnett River systems arise (Figure 2). The foot slopes occur at 400 m asl and the mountains rise to 1100 m asl at their summit. The higher elevations of the Bunya Mountains capture sufficient orographic rainfall to support notophyll rainforest (wet rainforest) with floristic and structural differences to the Auracarian microphyll vine forest (or dry rainforest) at lower elevations (Figure 3). There is some 4,500 ha of notophyll rainforest, 9,400 ha of dry rainforest, 13,800 ha of savanna woodland dominated by Forest Red Gum *Eucalyptus tereticornis* mainly at low altitudes (Figure 4) and Thin-leaved Stringybark *E. eugenioides* at higher altitude with grassy understoreys and 414 ha of grassland (Figure 5). Most, if not all plant species on the grassy balds also occur within the savanna woodlands. Grassy balds are mostly small relative to other primary habitat types, ranging from 0.1 ha to 44 ha in area. They are surrounded by one or more of the primary habitat types (Fensham and Fairfax 1996a, 1996b, 2006; Butler *et al.* 2006).

The grassy balds and savanna woodlands have been grazed by domestic livestock in the past, but there is no current grazing other than by native macropods such as Red-necked Wallaby *Macropus rufogriseus*. There has been a history of timber getting and plantation establishment, but no forests are currently harvested for timber (Humphries 1992). Visitors to the mountains mainly engage in nature recreation and use holiday houses and camping grounds primarily confined to a few localities; permanent residents are few.

Survey design

From February to April 2008, we surveyed four primary vegetation or habitat types (grassy balds, wet rainforest, dry rainforest and savanna woodland) and three mixed edge habitats (grassy bald-wet rainforest edge; grassy bald-dry

rainforest edge and; grassy bald-savanna woodland edge) for vertebrate fauna. Seven replicates were surveyed in each of the seven habitat types (or treatments): grassy bald, grassy bald-wet rainforest edge, wet rainforest, grassy bald-dry rainforest edge, dry rainforest, grassy bald-savanna woodland edge and savanna woodland, giving a total of 49 sites surveyed for vertebrate fauna (Figure 2).

Sites were set out as 100 metre x 50 metre (0.5 ha) plots. The edges of plots placed on grassy balds were at least 50

metres from the edge of the grassy bald. Grassy bald-forest sites were placed with the long axis of the plot along the interface between the distinct vegetation communities. Forest interior plots were located at least 100 metres from any grassy bald. Streams and other water bodies were avoided. Vertebrate fauna were surveyed using a variety of techniques over three days and nights involving direct observation, detection equipment and trapping; trapped animals were not marked and recaptures not identified.

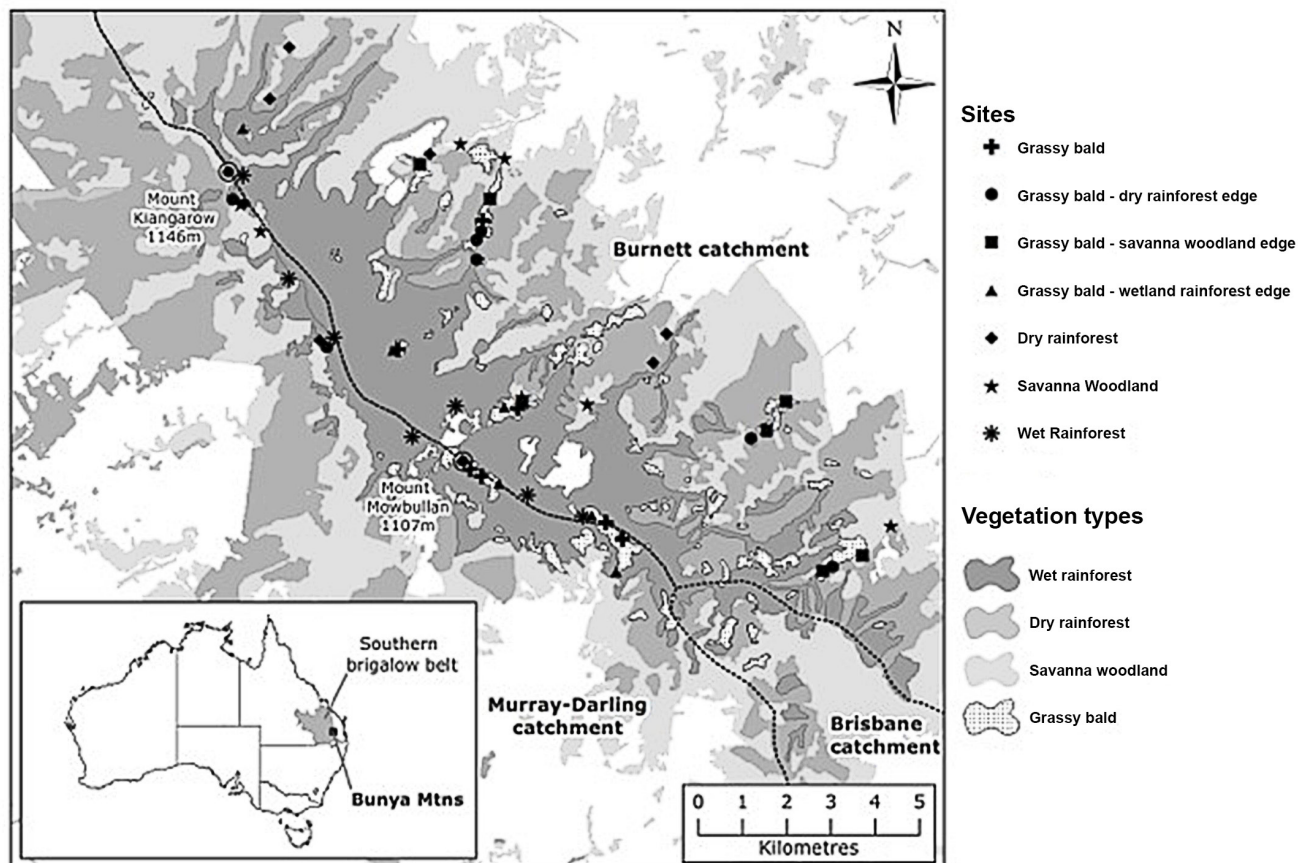


Figure 2. Map showing the location of the Bunya Mountains in the brigalow belt of south-east Queensland and the location of surveyed sites.



Figure 3. Araucarian microphyll vine forest, referred to as dry rainforest, occurs at lower altitudes. Hoop Pine *Araucaria cunninghamii* is the predominant *Araucaria* species in this vegetation type. Photo by Geoffrey Smith.



Figure 4. A savanna woodland containing *Eucalyptus tereticornis* with an understorey of tussock grasses similar to those present on grassy balds. Photo by Geoffrey Smith.



Figure 5. A typical grassy bald with rocks showing, indicating that soils can be shallow. Photo by Michael Mathieson.

The short period of sampling during one-off surveys in late summer-autumn at each site will have constrained our ability to detect all species in each location, but we aimed to offset this by our use of consistent methods between sites and our sampling regime across seven, spatially separated replicates per habitat type.

Birds were sampled in each 0.5 ha plot for 2 x 10 minute periods. One survey was carried out between dawn and 2 hours post-dawn and the other between 2 hours to 4 hours post-dawn. Bird species and numbers were recorded. Reptile searches were carried out in a 100 metre x 25 metre section of each plot by 2 observers using rakes and/or crowbars for 30 minutes (60 person-minutes), during daylight. Searches for nocturnally active vertebrates were implemented for 30 minutes by 2 observers (60 person-minutes) carrying spotlights and head torches over an area of 0.25 ha (100 metre x 25 metre sections of each 0.5 ha plot). Microbats were surveyed using electronic acoustic sampling and by trapping, but these data were not included in this analysis. Only the White-striped Mastiff-bat *Tadarida australis* was included in analyses, as these were detected by audible call; multiple calls were recorded as one individual, unless there were obvious spatially separate individuals vocal at the same time. Ground-dwelling mammals were targeted with 'Type A' Elliott™ traps deployed along the central line through the long axis of each 100 x 50 metre plot. Ten traps per site were placed evenly along the plot centre line, for 3 nights per site. Traps were baited with a "meat scented" bait and sweet potato coated in peanut oil. Reptile funnel traps were deployed within plots, utilising two separate, randomly placed, drift fences five metres long with funnel traps placed either side in the middle (i.e., two funnels per length of fence, four funnels in total per site), for three nights. Pit trapping was unviable in some locations due to the rocky substrate (Figure 5), so was not included in our methods in order to avoid inconsistency of trapping methods across sites. While pit traps generally capture more individuals of reptile species than funnel traps, funnel traps appear to capture more species of reptile than pits, particularly medium-sized skinks, dragon lizards and arboreal geckos and medium to large-sized terrestrial, diurnal snakes (Thompson and Thompson 2007; D. Ferguson personal



Figure 6. *Amalosia jacovae* is a moderately common gecko in the Bunya Mountains that is detected more through searching than trapping techniques. Photo by Michael Mathieson.

observation). There is some evidence that semi-fossorial lizards may avoid capture (Enge 2001), although other unpublished data suggests this is not always the case (D. Ferguson personal observation). More importantly, active searching by experienced observers can return more species (e.g., arboreal geckos; Figure 6) than both funnel and pit trapping combined (D. Ferguson personal observation).

Analysis

Species abundances were derived from summing records from each of the methods to give an overall figure for each species for each replicate. Total abundance of vertebrates for each replicate was obtained by summing across species. Comparisons of species richness and abundance values of vertebrates across habitats (treatments) were made using Kruskal-Wallis analysis (Siegel 1956).

Non-metric multidimensional scaling ordination (MDS) was used to compare vertebrate species assemblages recorded in each habitat type. Abundance data for each of the species were square-root transformed prior to the analyses to reduce the influence of more abundant species and then standardised by maximum values for each species. Ordinations were carried out using the Bray-Curtis similarity measure (Bray and Curtis 1957) in the Primer program (Clarke and Gorley 2006). The analysis of similarity (ANOSIM) routine in Primer was used to test for differences and similarities among species assemblages of treatments. Analyses were carried out comparing: 1. grassy bald, wet rainforest, dry rainforest and savanna woodland habitats, without edges; and 2. edge habitat with grassy bald, for wet rainforest, dry rainforest and savanna woodland habitats in three separate analyses so that each edge could be compared with its respective interior (i.e., grassy bald-wet rainforest edge-wet rainforest interior, grassy bald-dry rainforest edge-dry rainforest interior and grassy bald-savanna woodland edge-savanna woodland interior comparisons). The species predominantly responsible for the Bray-Curtis dissimilarities in the comparisons between habitats were determined using the SIMPER routine. The results were similar for bird only data and all vertebrate data; analyses including all vertebrates are presented in this paper.

Results

The numbers of terrestrial vertebrate species encountered on surveyed sites included 2 frogs (3 records), 20 reptiles (72 records), 86 birds (1954 records) and 11 mammals (54 records; excluding microbats as described in methods) (Table 1). One hundred and nineteen species were included in our analyses, with the majority of records (i.e., 93%) obtained from bird observations. Only one endemic species was found during the survey period, the Bunya Sunskink *Lampropholis colossus*. A further two other species of skink in this genus Dark-flecked Garden Sun-skink *L. delicata* and Friendly Sunskink *L. amacula* were also found. *L. colossus* was associated with grassy balds only at dry rainforest margins, with other observations of the species within dry rainforests and in moist savanna woodlands containing rainforest elements at higher altitudes on the mountains. *L. delicata* records were obtained from drier savanna woodland at lower altitudes and *L. amacula* observations were made at grassy bald-dry rainforest margin sites at separate sites to *L. colossus*. A further 22 species of reptile have been recorded in the Bunya Mountains (unpublished data, WildNet database, Queensland Government). While some of these are fossorial in habit, the reptile species detected from our study do not suggest that fossorial species were consistently overlooked by our methods.

The highest number of vertebrate species were associated with savanna woodland edge (66 species) and savanna woodland (65 species; Table 1), and the lowest with grassy balds (30 species). Species richness (Kruskal-

Wallis $H=20.1$, $df=6$, $P<0.01$) and abundance on grassy balds (Kruskal-Wallis $H=18.08$, $df=6$, $P<0.05$) were significantly lower than for any other habitat (Figure 7).

Multi-dimensional scaling ordination of species assemblages (Figure 8) and ANOSIM dissimilarity test statistics (Table 2) indicated that grassy balds were distinct from wet and dry rainforests and savanna woodland. Wet rainforests differed from dry rainforest ($R=0.5$, $P=0.001$) and savanna woodland ($R=0.5$, $P=0.003$), while dry rainforests could not be distinguished from savanna woodland ($R=0.1$, $P=0.2$).

Further analysis comparing primary habitat types with edges (Table 3) indicated that grassy balds were significantly different from all edge habitats in their species assemblages and that wet and dry rainforest interiors were significantly different from their respective edges. Savanna woodland interiors did not differ significantly from savanna woodland edge suggesting that fauna made no distinction between savanna woodland interior and savanna woodland edge.

SIMPER analysis showed that wet rainforest separated from dry rainforest and savanna woodland species assemblages mainly because of bird, but also because of two mammal species (Table 4). Differences between rainforest edges and rainforest interiors were largely due to differences in bird abundances and to some extent species composition (Table 4).

Grassy bald species assemblages were separated from

Table 1. Number of species (and records of those species) associated with each of the habitats.

| Species richness | Grassy bald | Wet Rainforest Edge | Wet Rainforest | Dry Vine Forest Edge | Dry Vine Forest | Savanna Woodland Edge | Savanna Woodland |
|------------------|----------------|---------------------|-----------------|----------------------|-----------------|-----------------------|------------------|
| Frogs | 0 | 0 | 1 (1) | 0 | 1 (2) | 0 | 0 |
| Reptiles | 5 (8) | 2 (3) | 1 (1) | 8 (9) | 2 (4) | 7 (20) | 9 (27) |
| Birds | 23 (84) | 37 (267) | 36 (272) | 45 (292) | 43 (316) | 58 (367) | 51 (356) |
| Mammals | 2 (2) | 3 (17) | 3 (16) | 5 (12) | 0 | 1 (1) | 5 (6) |
| TOTAL | 30 (94) | 42 (287) | 41 (290) | 58 (313) | 46 (322) | 66 (388) | 65 (389) |

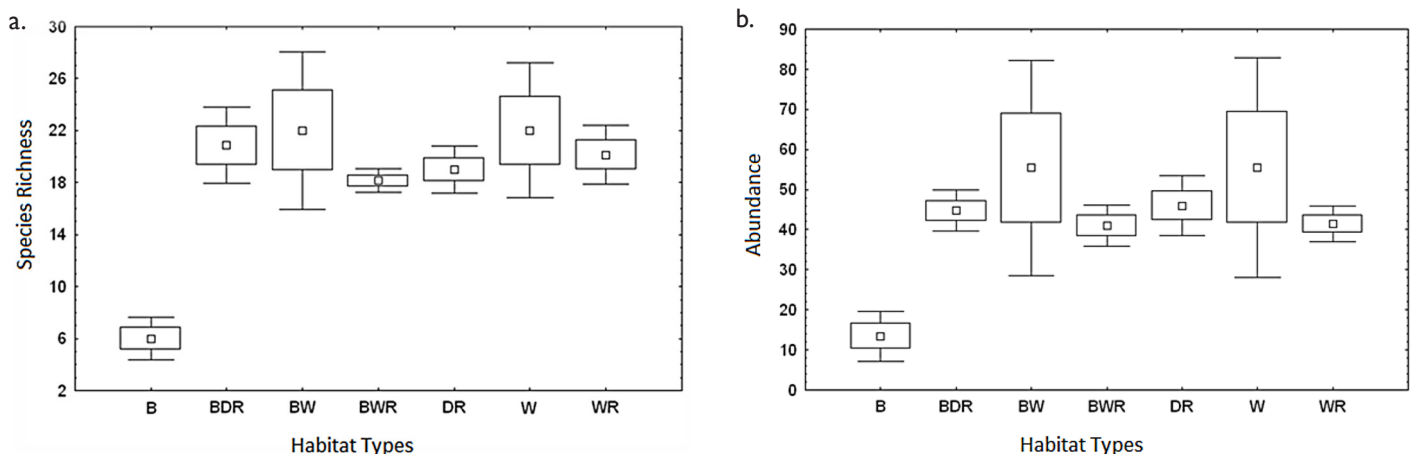


Figure 7. a. Species richness of vertebrates (vertical axis) recorded among sites shown by habitat categories. b. Abundance of vertebrates (vertical axis) recorded among sites shown by habitat categories. Box and whiskers show standard errors (SE) and $\pm 1.96SE$. B= grassy balds, BDR= grassy bald-dry rainforest edge, BW= grassy bald-savanna woodland edge, BWR= grassy bald-wet rainforest edge, DR= dry rainforest interior, W= savanna woodland interior, WR= wet rainforest interior.

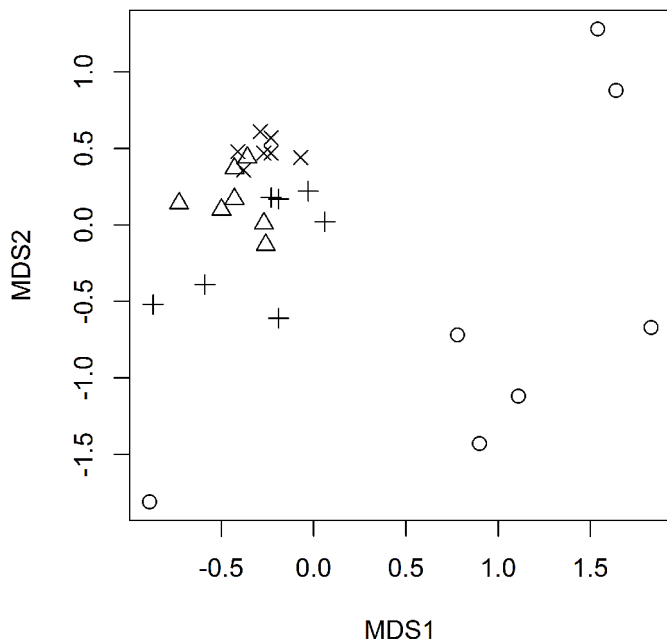
Table 2. ANOSIM dissimilarity test statistics from pair-wise comparisons of primary vegetation types. Table contains R statistic and level of significance in parenthesis.

| Forest type | Wet rainforest | Dry rainforest | Woodland |
|----------------|------------------|------------------|------------------|
| Grassy bald | 0.550 (0.001)*** | 0.556 (0.002)*** | 0.443 (0.002)*** |
| Wet Rainforest | | 0.485 (0.001)*** | 0.484 (0.003)*** |
| Dry rainforest | | | 0.079 (0.172) NS |

forest, woodland and edge assemblages mainly because of birds associated with the upper and mid forest strata in the latter (Table 4). Many of the ground and lower strata bird species typically associated with rainforest avoided grassy balds, while other lower strata associating species such as Superb Fairy-wren *Malurus cyaneus* and Red-browed Finch *Neochmia temporalis* were significantly associated with grassy balds but avoided rainforests. Another five grassy bald species were found only at grassy bald sites, but only three of these Golden-headed Cisticola *Cisticola exilis*, Common Dunnart *Sminthopsis murina* and Eastern Chestnut Mouse *Pseudomys gracilicaudatus* are likely to be grassland preferring species (Table 4). These uncommon grassland species, together with those significantly associated with grassy balds, made up some 4% of all species encountered. In effect, most of the 30 species occurring on grassy balds, were habitat generalists occurring in rainforest, savanna woodland and/or edge habitat.

Discussion

While this study did not detect all of the vertebrate

**Figure 8.** Multi-dimensional scaling ordination of the primary vegetation type sites based on faunal community similarity/dissimilarity. 0 = grassy bald, Δ = dry rainforest, + = savanna woodland, x = wet rainforest.**Table 3.** ANOSIM dissimilarity test statistics from pair-wise comparisons of grassy balds with edges for each forest category. Table contains R statistic and level of significance in parenthesis.

| Forest/habitat type | Grassy bald vs Edge | Edge vs Forest/Savanna woodland interior |
|---------------------|---------------------|--|
| Wet rainforest | 0.578 (0.002)*** | 0.185 (0.039)*** |
| Dry rainforest | 0.578 (0.003)*** | 0.259 (0.001)*** |
| Savanna woodland | 0.555 (0.002)*** | -0.061 (0.725) NS |

species listed from the Bunya Mountains, which is comprised of approximately 300 native vertebrate species, including more than 20 bat species (unpublished data, WildNet database, Queensland Government), our work is significant in that it is the first study to systematically assess vertebrate communities across major vegetation types. Consequently the study has demonstrated that the fauna on the Bunya Mountains is largely patterned in response to the structural formations of the diverse vegetation. However, some vegetation types that are floristically and structurally distinct, such as dry rainforest and savanna woodland, had similar fauna composition. Grassy balds are structurally simple and distinct from other vegetation types studied and contained the lowest diversity of species of any of the vegetation types considered. There were very few, grassland specialising species occurring on the grassy balds; the assemblage mainly comprised species that occurred in other habitats. The lack of specialist fauna on grassy balds is consistent with historical explanations of the origins of grassy balds, but could also be explained by their small size and relative structural simplicity. Forest margins, at the boundary between grassy balds and rainforests were found to exert an edge influence over faunal assemblages.

Rainforests and savanna woodlands

Higher elevation in addition to the floristic and physiognomic differences of wet rainforest is likely to have led to the distinct faunal assemblage in wet rainforest compared to dry rainforest and savanna woodland (Kikkawa 1982). However, the faunal similarity between dry rainforest and savanna woodland in the Bunya Mountains is remarkable given their contrasting floristic and structural composition. A number of habitat generalists were common to both vegetation types. Dry rainforests share a number of species with savanna woodlands firstly because they are embedded within the larger matrix of savanna woodlands at lower altitudes on the mountain range and secondly because a large proportion of the fauna species utilise the mountain slopes on a seemingly broad scale. The monsoon rainforests within the tropical savannas of northern Australia were similarly patterned to our dataset, with the moister forests mostly comprised of species from adjacent savanna habitats with only few specialised vertebrates (Woinarski 1993). Although dry rainforests possess a number of ground-feeding specialists that include some pigeon species, as well as the Black-breasted Button-quail *Turnix melanogaster*, these species

Table 4. Species characterising each of the habitat types. † indicates species significantly associated with habitat types using SIMPER analysis; the list includes only the topmost species contributing cumulatively up to 50% of explained variance. * indicates species found in low numbers only in the specified habitat.

| Species characterising grassy balds | Species characterising wet rainforest | Species characterising dry rainforest/savanna woodland | Species characterising wet rainforest edges | Species characterising dry rainforest edges |
|---|---|---|---|---|
| †Superb Fairy-wren <i>Malurus cyaneus</i> , | †Brown Cuckoo-dove <i>Macropygia amboinensis</i> , | †Emerald Dove <i>Chalcophaps indica</i> , | †Fan-tailed cuckoo <i>Cacomantis flabelliformis</i> , | †Rose robin <i>Petroica rosea</i> , |
| †Red-browed Finch <i>Neochmia temporalis</i> , | †Green Catbird <i>Ailuroedus crassirostris</i> , | †Laughing Kookaburra <i>Dacelo novaeguineae</i> , | †Grey Shrike-thrush <i>Colluricincla harmonica</i> , | †Grey Shrike-thrush <i>Colluricincla harmonica</i> , |
| *Golden headed <i>Cisticola Cisticola exilis</i> , | †Rufous Fantail <i>Rhipidura rufifrons</i> , | †Grey Fantail <i>Rhipidura fuliginosa</i> , | †White-throated Treecreeper <i>Cormobates leucophaeus</i> , | Paradise Riflebird <i>Ptiloris paradiseus</i> , |
| *Common Dunnart <i>Sminthopsis murina</i> , | †Yellow-throated Scrubwren <i>Sericornis citreogularis</i> , | †Grey Shrike-thrush <i>Colluricincla harmonica</i> , | †Pied Currawong <i>Strepera graculina</i> , | †Fan-tailed Cuckoo <i>Cacomantis flabelliformis</i> , |
| *Eastern Chestnut Mouse <i>Pseudomys gracilicaudatus</i> . | †Brown Gerygone <i>Gerygone mouki</i> , | †Cicadabird <i>Coracina tenuirostris</i> , | †Brown Thornbill <i>Acanthiza pusilla</i> , | †Satin Bowerbird <i>Ptilonorhynchus violaceus</i> , |
| | †Eastern Spinebill <i>Acanthorhynchus tenuirostris</i> , | †White-throated Treecreeper <i>Cormobates leucophaeus</i> , | †Wonga Pigeon <i>Leucosarcia melanoleuca</i> , | †Eastern Spinebill <i>Acanthorhynchus tenuirostris</i> . |
| | †Eastern Yellow Robin <i>Eopsaltria australis</i> , | †Pied Currawong <i>Strepera graculina</i> , | †Satin Bowerbird <i>Ptilonorhynchus violaceus</i> , | |
| | †Bobuck <i>Trichosurus caninus</i> , | *Black-breasted Button-quail <i>Turnix melanogaster</i> . | †White-browed Scrubwren <i>Sericornis frontalis</i> . | |
| | †White-striped Freetail bat <i>Tadarida australis</i> . | | | |

were not in sufficient numbers to distinguish dry rainforest assemblages from savanna woodland in the analyses.

Grassy balds

The fauna of the grassy balds was depauperate in both species and abundance of animals compared with the wet rainforest, dry rainforest, savanna woodland and the edge habitats between grassy balds and the wooded environments. This response was largely patterned by the bird fauna which numerically dominated our observations, supplemented by the contributions of a few reptile and mammal species. In general the species encountered on grassy balds were a subset of species observed in other habitats. They comprised species which were frequently associated with the lower stratum vegetation, the ground substrate of wooded habitats and the grassland communities of the savanna woodland, such as the insectivorous or granivorous *Malurus cyaneus* and *Neochmia temporalis*.

Species diversity, particularly among birds, is tied closely to the structural complexity of vegetation and the physical structure of forests (Holmes et al. 1979; MacNally 1990; Whelan 2001; Kutt and Martin 2010). Floristically and structurally, grassy balds are characterised by a dense layer of tussock grasses with little exposed substrate or leaf litter. Few shrubs and no trees occur on these grassy balds. They are both floristically and structurally different to the wooded interior habitats and to edges with these habitats. The diversity of plants in grassy balds is lower than wooded habitats (Butler et al. 2006) and the structural complexity is simple compared with other habitats. Food resources in grassy balds are likely limited to grass seed for granivores,

herbage for herbivores, insects for insectivores and prey for raptors that feed in open fields, while the resources produced in the floristically diverse forests such as nectar from flowering plants, fleshy fruits, foliage for browse and fungi are scarce. Grassy balds are also limited in the structural features that are abundant in wooded environments that provide habitat for many vertebrates, such as hollows in trees for hollow-dependent fauna, standing wood and bark that is important for many reptiles and birds and leaf litter for ground feeding species. Furthermore, grassy balds on the Bunya Mountains massif are small fragments of habitat in a matrix of wooded habitat and may be too small to support species that have large area requirements (MacArthur and Wilson 1967; Hargis et al. 1999) or a specialised fauna, such as the grassland species associated with cracking clay soils, which include species such as the Five-clawed Worm-skink *Anomalopus mackayi*, Grassland Earless Dragon *Tympanocryptis pinguicolla*, Narrow-nosed Planigale *Planigale tenuirostris* and the Long-tailed Planigale *P. ingrami* (Butler 2007). Few, if any of the species listed for the Bunya Mountains (WildNet database, Queensland Government) that were not detected in this study, could be considered grassland specialists.

The few species of animals and the lack of specialists on grassy balds suggest that if they were to disappear there would be little biodiversity loss. Many species could in fact be retained in other wooded vegetation, particularly savanna, were it not to succumb to rainforest invasion. Butler et al. (2006) have previously proposed that many grassy bald plant species may survive in savanna woodland should balds disappear. However if grassy balds are considered

in the context that they also provide edge habitat for a number of species that require this association, then their loss may lead to changes in community structure beyond just the loss of grassland habitat.

Edge habitats

In the Bunya Mountains, all edge habitat fauna assemblages were significantly different to grassy balds. However of greater significance is that rainforest edge communities were significantly different from their respective rainforest interiors. These edge responses were mainly driven by disparities among species abundances rather than the presence of edge specialists.

Edge vegetation at the grassy bald-rainforest transition zone forms a solid curtain of vegetation tending to have well developed vegetation at tree and shrub layers (Figure 1). While ground layer vegetation is thick proximal to the grassy bald and ground vegetation is sparse proximal to the forest side of the edge. The gradient is steep and the transition zone narrow. The influence of the edge on biotic communities appears to be moderated by patch contrast, the complexity of vegetation structure and the permeability of the edge to organism flow and is more apparent where there is a high level of contrast between adjacent patches (Lidicker 1999; Strayer *et al.* 2003; Harper *et al.* 2005).

Unlike rainforest edges, there was limited distinction between the fauna of savanna woodland edges and savanna woodland interiors and it is likely that this relates to the transition from grassy bald into savanna woodlands being less stark. There is no thick curtain of dense trees and shrubs, and the grassy ground layer is continuous from grassy bald to woodland. There is furthermore a broad overlap in the floristic composition of grassy bald and savanna woodland (Butler *et al.* 2006; Figure 4). Thus fauna species are more able to traverse the boundaries between grassy bald and savanna woodland interior than across bald-rainforest boundaries.

Grassy bald fauna – maintenance and management

Grassy balds contribute a small number of species to biodiversity across the landscape, while edges provide sufficient heterogeneity in the landscape to create further variation in species assemblages. Based on this study, there is a small justification for the retention of grassy balds and their edges to maintain vertebrate biodiversity in the landscape. However, if these landscape features are to be maintained then it is likely that fire management as advocated by Fensham and Fairfax (2006) may be the best available option. They argue that fire has been used to maintain these grassy balds through the Holocene.

Bond and Parr (2010) suggest that distinct suites of flora and fauna associate with grassland biomes of considerable antiquity. If the grassy balds were an ancestral vegetation that was more widespread in the Pleistocene (Webb 1964), then one might expect specialist relictual species to have survived. Alternatively the grassy balds have likely had a more recent origin and have always been limited in extent, supporting the idea that grassy balds and their fauna have been shaped by recent phenomena, postulated to be fire (Fensham and Fairfax 2006). Our studies returned only one species endemic to the Bunya Mountains which was not strictly associated with grassy balds. While the taxonomy of this endemic species *Lampropholis colossus* and its relationship with other congeners is currently under study (C. Hoskin pers. comm. 2014, JCU) we continue to accept that it is a species that has probably evolved on this mountain top in ancient rainforest vegetation with which it is now primarily affiliated (Ingram 1991). The paucity of endemic specialists on grassy balds therefore supports theories of their more recent origins.

Work by Fensham and Fairfax (2006) and Fairfax *et al.* (2009) has shown that grassy balds can be preserved using fire as a tool where they adjoin rainforest, but that preservation by burning is not necessarily a viable option where grassy bald adjoins savanna woodland. Our study suggests that maintenance of edges at grassy bald-rainforest interfaces using fire will create greater heterogeneity in the landscape to the benefit of fauna than preservation of savanna woodland edges abutting grassy balds. Burning grassy balds adjacent to rainforests on 2-3 year cycles should therefore be a priority in order to maintain maximal fauna diversity across the Bunya Mountains landscape.

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